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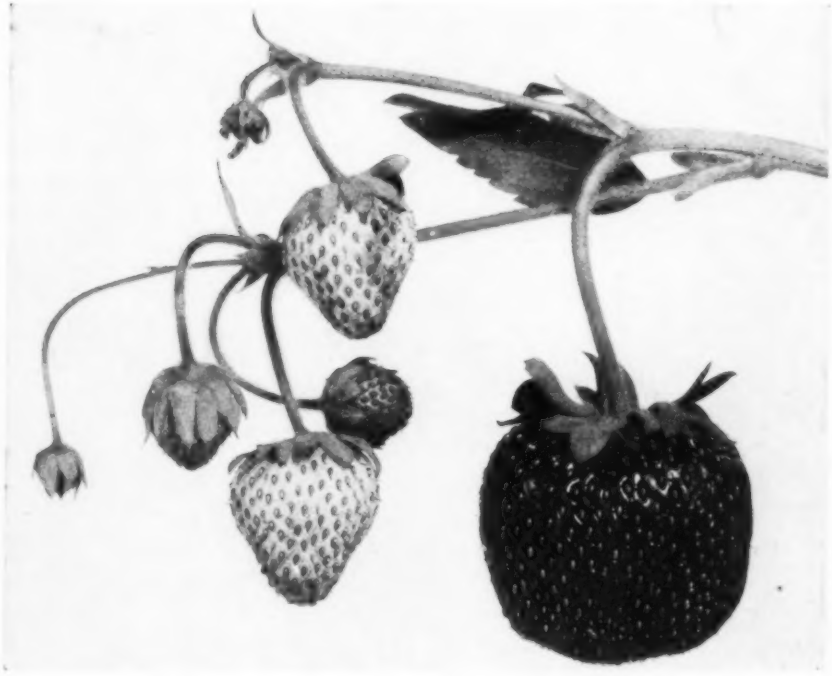

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(SEE PAGE 481)

Charles Darwin's Diary

Inheritance of Blood Groups in the Rabbit

Inheritance of "Hollow Chest"

History of Cultivated Plants

VOLUME 25 NOVEMBER, 1934 NUMBER 11

The American Genetic Association

An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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The

Journal of Heredity

Vol. XXV NOVEMBER, 1934 No. 11

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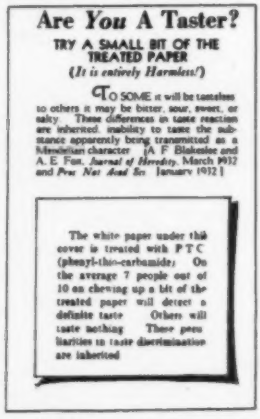
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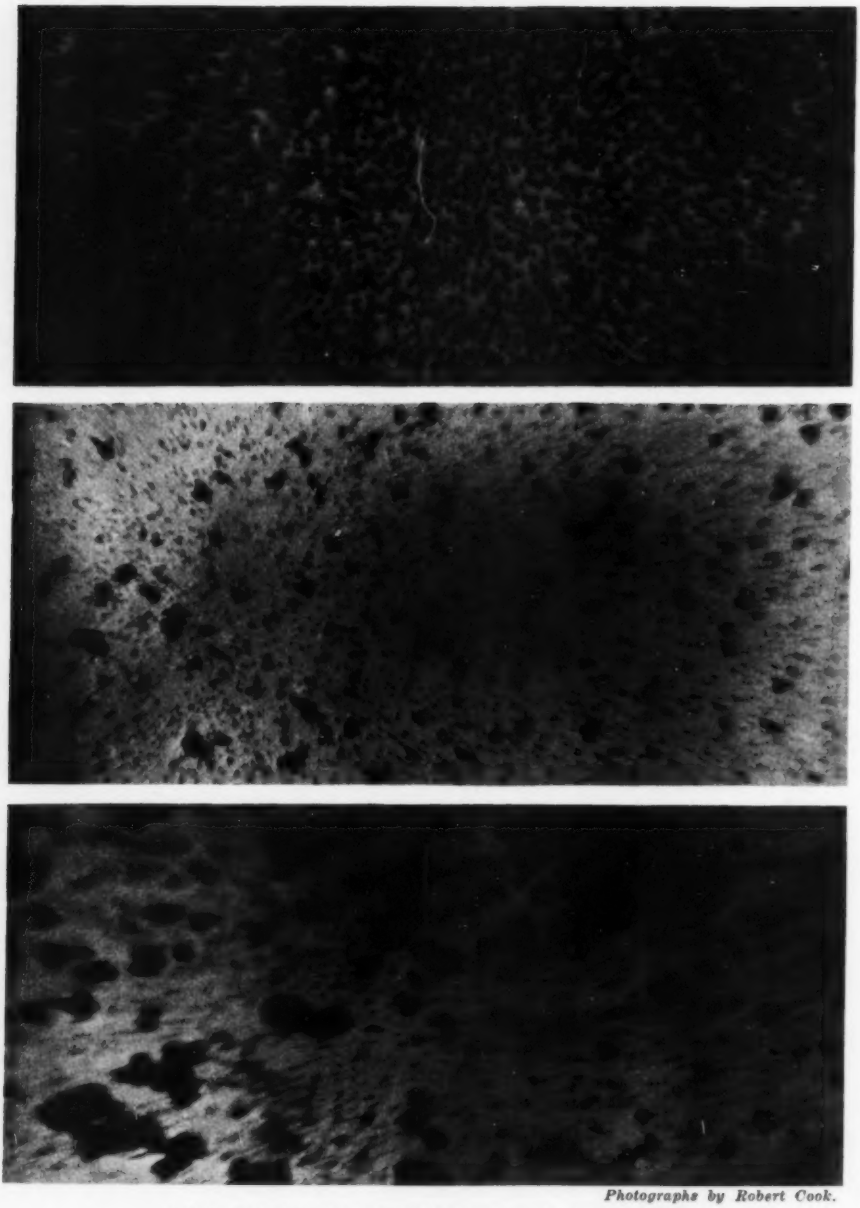


Photographs by Robert Cook.

AGGLUTINATION OF INCOMPATIBLE BLOODS

Frontispiece

The differences in blood known as the "blood groups" occur in several species of mammals. Classification of these groups is based on the phenomenon of agglutination. When compatible bloods are mixed no agglutination occurs (See upper photograph). When incompatible bloods are mixed, agglutination or clumping of the red blood cells takes place, as is shown in the two lower views, which illustrate two stages in the agglutination of a mixture of *A* and *B* bloods of man. This phenomenon was discovered by Dr. Karl Landsteiner in 1900. It has great practical importance in medicine, since the transfusion of incompatible blood is often fatal to the recipient. That the mendelian laws of inheritance apply to the blood groups is recognized by the courts of many countries and in some instances definite conclusions are possible in cases of disputed paternity.

BLOOD GROUP INHERITANCE IN RABBITS

C. E. KEELER and W. E. CASTLE
Howe Laboratory and Bussey Institution, Harvard University

WHAT are known as blood groups occur in certain species of mammals, including man. The individuals of a blood group are alike in the constitution of their blood, and blood from individuals of the same group may be mixed, as in transfusion, without the occurrence of agglutination or clumping of the blood cells. Such agglutination occurs only when samples of blood from individuals of different and incompatible groups are mixed. Hence, in man, determination of the blood group of donor, and usually of recipient also, is necessary before transfusion can safely be performed.

Agglutination results from a twofold agency consisting of (1) an agglutinogen carried in the red blood cells of the donor and (2) an agglutinin carried in the blood plasma of the recipient. If either is lacking, no agglutination will occur. Thus a donor's blood may carry agglutinogen *A*, but if the recipient's plasma *does not* carry the corresponding agglutinin *a*, transfusion may safely be made, since no agglutination will occur. Or if the recipient's plasma contains agglutinin *a*, but the donor's blood cells lack agglutinogen *A*, no agglutination will occur.

Conventionally, in harmony with the Ehrlich symbolism, we may represent in diagrams an agglutinogen as a receptor cavity in a blood cell into which will fit only a similarly shaped agglutinin, the fitting together of the two being employed to express the occurrence of agglutination.

With the aid of such diagrams (Figure 1) we propose to describe certain blood group phenomena of rabbits.

In rabbits there are four blood groups, and their characteristics are shown in Figure 2. At the left in the figure is shown a rabbit whose blood cells contain no agglutinogen. In the rectangles below are shown the effects of mixing blood from such a rabbit with serum which contains either h_1 agglutinin (upper rectangle) or h_2 agglutinin (lower rectangle). No agglutination occurs in either case because no agglutinogen is present.

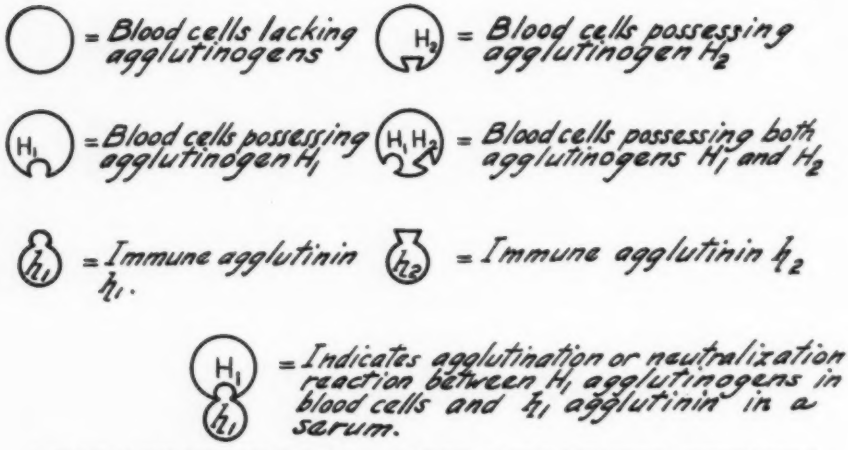
The next rabbit to the right in Figure 2 possesses H_1 agglutinogen. In the rectangle below is shown the occurrence of agglutination in the presence of h_1 agglutinin, but not of h_2 agglutinin (lower rectangle).

The next rabbit in Figure 2 possesses H_2 agglutinogen, and agglutination is seen to occur only when h_2 agglutinin is added.

The fourth rabbit in Figure 2 possesses both H_1 and H_2 agglutinogens, and its blood is agglutinated by either h_1 or h_2 agglutinin. These four kinds or "groups" of rabbits we may designate the *zero* group, the H_1 group, the H_2 group, and the H_1H_2 group.

Production of Agglutinins

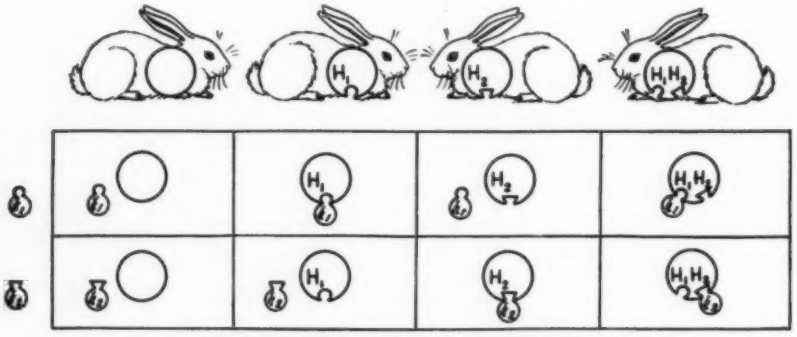
The agglutinins are not present in the blood plasma of ordinary, untreated rabbits in sufficient strength to produce agglutination of foreign blood. Perhaps they are not present there at all. But their formation can be artificially stimulated or induced by the introduction of blood cells containing an agglutinogen not possessed by the recipient. In that case the corresponding agglutinin arises as an immune reaction. These statements are shown pictorially in Figure 3. The rabbit at the left has H_1 agglutinogen as indicated by the receptor cavity in a red blood cell. If this blood is injected into a *zero* rabbit (shown at the right), h_1 agglutinin is produced in its serum. The blood of such a rabbit is diagrammed below, where is shown h_1 agglutinin mingled with *zero* blood cells, but the two do not combine. Yet if serum from the injected rabbit (containing h_1 agglutinin) is now mixed


= Blood cells lacking agglutinogens
= Blood cells possessing agglutinogen H_2
= Blood cells possessing agglutinogen H_1
= Blood cells possessing both agglutinogens H_1 and H_2
= Immune agglutinin h_1.
= Immune agglutinin h_2
= Indicates agglutination or neutralization reaction between H_1 agglutinogens in blood cells and h_1 agglutinin in a serum.

A DIAGRAMMATIC OUTLINE OF BLOOD AGGLUTINATION MECHANISM

Figure 1

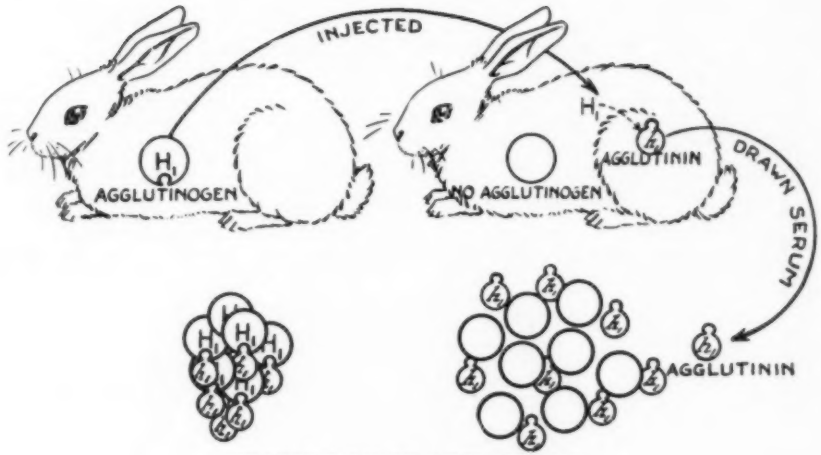
There are four types of blood cells, depending on whether they lack agglutinogens, or carry either agglutinogen H_1 or H_2 or both. The agglutinins are distinct substances, which react with the agglutinogens to cause agglutination, or clumping of the blood cells when incompatible bloods are mixed. In man also four main blood groups are known (and at least two sub-groups). While the mechanism of inheritance and agglutination appears to be the same in men and in rabbits, the agglutinative substances are different. That is, the H_1 and H_2 agglutinogens of rabbits are not the same as the A and B agglutinogens in man.



FOUR BLOOD GROUPS IN THE RABBIT

Figure 2

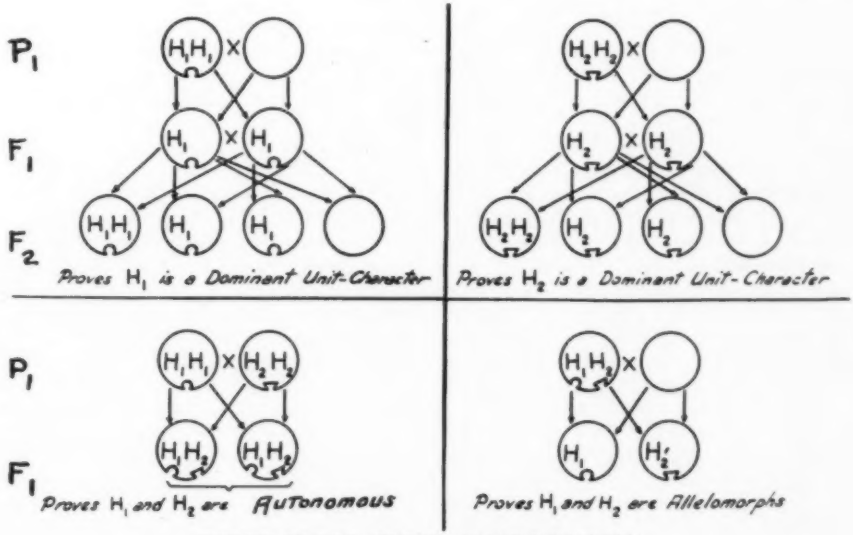
As in man, four blood groups have been found in the rabbit. And as highly probable in man, the inheritance of these four blood types is due to a series of three allelomorphic genes. Here are shown the four types—*"zero"* (with no agglutinogens), H_1, H_2, and H_1H_2. Below are shown the results obtained by mixing the blood of these rabbits with a serum which contains either agglutinin h_1 or h_2. See text for detailed description.



PRODUCTION OF AGGLUTININS

Figure 3

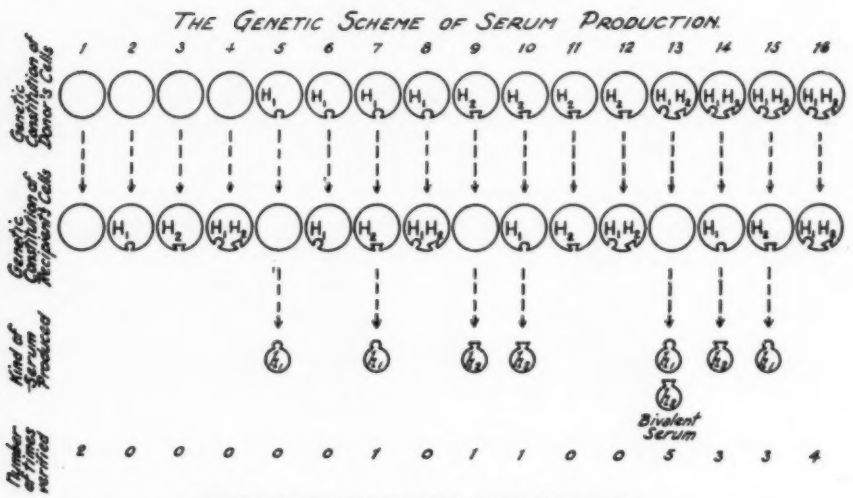
The blood of an ordinary rabbit does not contain enough agglutinin to produce agglutination of incompatible foreign blood. By blood transfers it is possible to stimulate the production of agglutinin, so that agglutination can be demonstrated. Thus H_1 blood injected into a *"zero"* rabbit produces h_1 agglutinin which may be used to agglutinate the blood of the donor.



THREE BLOOD GROUP ALLELOMORPHS

Figure 4

The two agglutinogens are transmitted as mendelian characters, each dominant to the non-agglutinating *zero* type, and each of them functional when both are present in the same individual. These four crosses demonstrate the mendelizing nature of these characteristics.


THE GENETIC SCHEME OF SERUM PRODUCTION
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Genetic Constitution of Donor's Cells
Genetic Constitution of Recipient's Cells
Kind of Serum Produced
Bivalent Serum
Number of Times Verified
2 0 0 0 0 0 1 0 1 1 0 0 5 3 3 4

RESULTS OF INJECTION EXPERIMENTS

Figure 5

Sixteen combinations of the four blood groups are possible. These should yield either no agglutinin, or one or both of the h_1 or h_2 type. Half of these theoretical combinations have thus far been verified by experiment, and no exceptions found as yet (lower row).

with blood of the donor, or with blood of any other rabbit of the same group, agglutination occurs, as indicated in the space below the donor in Figure 3.

Inheritance

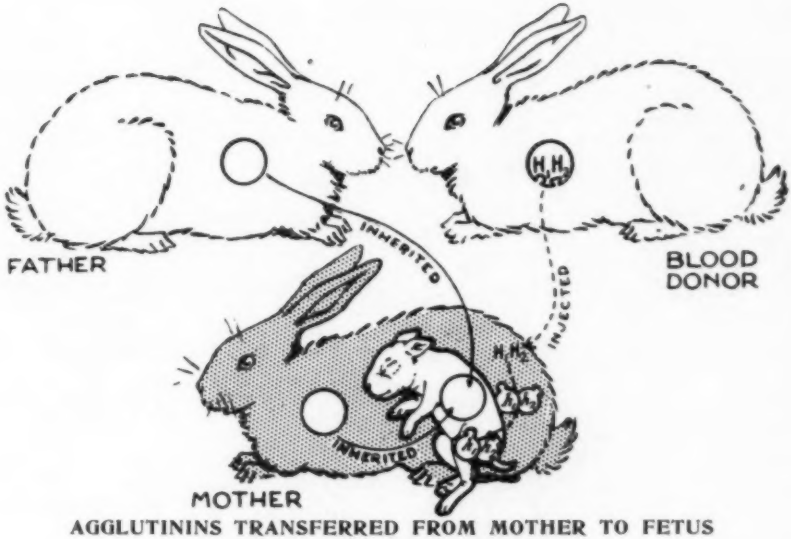
In heredity the agglutinogens are transmitted as dominant characters, H_1 and H_2 being allelomorphs. The results of various types of matings are diagrammed in Figure 4, the nature of the individual being shown by a blood cell in which is indicated its agglutinogen content. The upper left diagram of Figure 4 shows that a mating between a homozygous H_1 individual and a *zero* individual produces in F_1 heterozygous H_1 individuals, and in F_2 one homozygous H_1 individual, two heterozygous H_1 individuals, and one *zero* individual, in complete conformity with Mendel's law.

The upper right diagram of Figure 4 shows, in a similar way, the result of a mating between a homozygous H_2 rabbit and a *zero* rabbit. F_1 consists of heterozygous H_2 animals exclusively, and F_2 consists of homozygous H_2, heterozygous H_2, and *zero* animals in a 1:2:1 ratio.

The lower left diagram of Figure 4 indicates that a cross between a homozygous H_1 and a homozygous H_2 animal produces only H_1H_2 offspring in F_1.

The lower right diagram indicates that such H_1H_2 individuals transmit H_1 and H_2 in separate gametes, since, when mated with a *zero* individual, only heterozygous H_1 or heterozygous H_2 offspring are produced. In other words, H_1 and H_2 are allelomorphs.

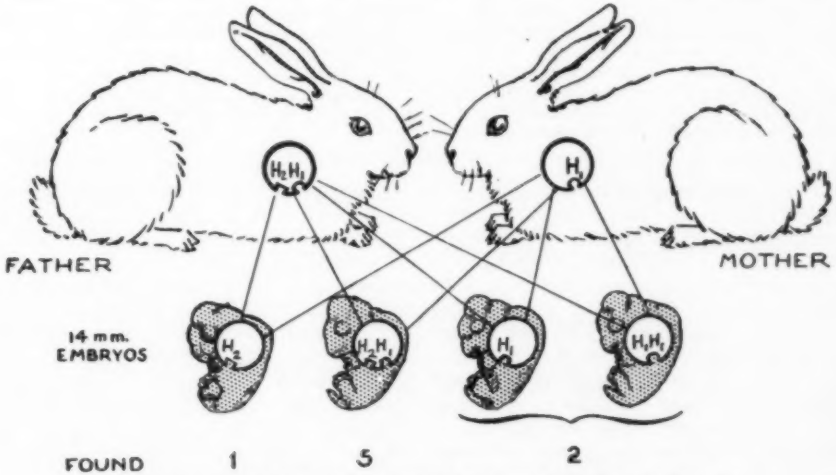
Although H_1 and H_2 are allelomorphs, neither one by its presence interferes with the action of the other. Each produces its specific antibody whether the other is present or not. This is indicated in Figure 5 which summarizes the results of numerous injection experiments. The expected results of sixteen different sorts of blood transfer are shown. The top row shows the blood-cell character of the donor, the next lower row shows the character of the recipient, and the third row shows



AGGLUTININS TRANSFERRED FROM MOTHER TO FETUS

Figure 6

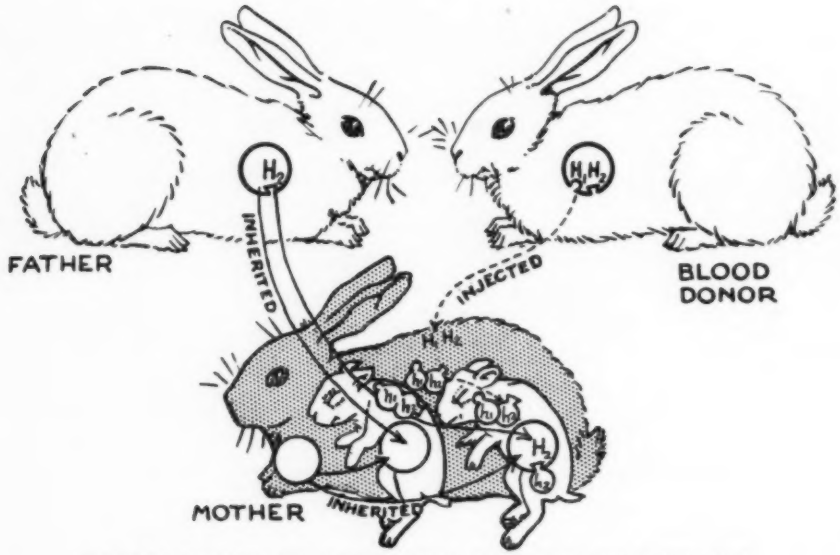
A *zero* mother, injected with H_1H_2 blood develops both h_1 and h_2 agglutinins in her blood, (as can be demonstrated by appropriate tests), and these agglutinins are transmitted through the placenta to her offspring. (See text.)



DEVELOPMENT OF AGGLUTINOGEN IN YOUNG EMBRYOS

Figure 7

This drawing gives in diagram the outcome of an experiment demonstrating the existence of agglutinogens in the blood of embryos of 14 mm. body length. The father possessed both agglutinogens (H_1 and H_2); the mother possessed H_1 only. The young, as expected, were of three sorts, H_1 (two individuals either heterozygous or homozygous), H_2 (one individual), and H_1H_2 (five individuals). A later experiment made upon still younger embryos of only 4 mm. body length showed that agglutinogens were already developed in their nucleated blood cells (normoblasts).



BLOOD INCOMPATIBILITIES NOT HARMFUL TO EMBRYOS

Figure 8

Above is diagrammed an experiment to ascertain whether detriment may accrue to an embryo inheriting from its father an erythrocyte constitution incompatible with the agglutinin content of the mother's blood plasma. The mother, prior to and during pregnancy, received injections of blood which would produce in her an agglutinin antagonistic to an agglutinogen borne by half of her young through inheritance from their father. In three such litters of young, including 14 individuals, there were 9 individuals having incompatible erythrocytes, but no agglutination or other harmful result ensued.

the resulting agglutinin formation (if any) in the plasma of the recipient. Note that univalent serum (either h_1 or h_2) results in six out of seven categories of blood transfer expected to yield positive results, but that bivalent serum (containing both h_1 and h_2 agglutinin) results only when H_1H_2 blood is injected into a *zero* recipient. A mixture of H_1 and H_2 blood would be equally effective. The fourth row of Figure 5 shows the number of independent experiments in which the result indicated was observed. A zero entry in that row indicates that that particular transfer was not made, but theoretically should give the result diagrammed.

An experiment which shows that agglutinins formed in a mother's blood pass freely through the placenta into the blood plasma of her young *in utero* is diagrammed in Figure 6. A *zero* group mother rabbit receives injections of H_1H_2 blood from a donor (upper right, Figure 6) and develops h_1 and h_2 agglutinins in her blood plasma. At the same time she has become pregnant by mating with a buck also of *zero* group like herself. The young consequently, one of which is shown in the diagram, will also be *zero* animals as indicated. But when a sample is taken of the blood of the young, it is found to have the same agglutinative properties as the mother's blood, causing agglutination both of H_1 blood cells and of H_2 blood cells. In other words, it contains both the h_1 and the h_2 agglutinins, which can have been derived only from the mother's blood.

Since agglutinogens were present in

embryo in as early a stage of development as 14 mm. (see Figure 7), and since agglutinins were transmitted through the placenta, it seemed likely that incompatibilities between mother and fetus might be demonstrated by appropriate matings. An experiment testing this possibility is diagrammed in Figure 8. Since no adverse reactions were noted it appears that some protective medium is operative which prevents the disastrous results that theoretically would be expected.

Other experimental studies of the blood groups of rabbits might be diagrammed in a similar way, but these would lead us into matters of too technical a character for presentation in this place, where interest naturally centers on the fact that blood group inheritance, both in man and the lower animals, depends upon the transmission of a gene or genes borne in chromosomes, which lead to the production of agglutinogens in the red blood cells. The agglutinins, at least in rabbits, are secondarily produced and complementary structures.

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1. Castle, W. E. and C. E. Keeler. 1933. *Proc. Nat. Acad. Sci.*, Vol. 19, pp. 92-98; 98-100.

2. Keeler, C. E. and W. E. Castle. 1933. *Proc. Nat. Acad. Sci.*, Vol. 19, pp. 403-411.

3. ———— 1934. *Proc. Nat. Acad. Sci.*, Vol. 20, pp. 273-276; 465-470.

◆

Books Received

BOOKS are acknowledged in this column as received, and such acknowledgment must be regarded as sufficient return for the courtesy of the sender. As far as space permits, books that contain material of special interest to the readers of the JOURNAL *will be reviewed in later numbers.*

GRUNDRISS DER GARTNERISCHEN PFLANZENZUCHTUNG, *by* H. Kappert. Pages, 146, index, 29 illustrations, Rm. 6,80. Paul Parey, Berlin, 1934.

A compendium of horticultural genetics and breeding.

ALLGEMEINE PFLANZENKARYOLOGIE, *by* Dr. Georg Tischler. Pages 630, index, bibliography, 252 illustrations, Rm. 76.80. Verlag von Begruder Borntraeger, Berlin, 1934.

An extensively illustrated textbook of plant cytology.

PHYSICO-CHEMICAL PROPERTIES OF PLANT SAPS IN RELATION TO PHYTOGEOGRAPHY, *by* J. Arthur Harris, late head of the Department of Botany, University of Minnesota. Compiled from original records and edited by a committee of Dr. Harris' colleagues in the University of Minnesota. Pages 339, price $4.50. The University of Minnesota Press, Minneapolis, 1934.

Some 12,000 analyses of plant saps made by Dr. Harris during a twenty-year study persued when opportunity offered. "The most comprehensive study of the physiological adjustment of the plant to its environment."

DYNAMICS OF POPULATION, *by* Frank Lorimer and Frederick Osborn. Pages 375 with 85 pages of bibliography, tables and charts. Price $4.00. The Macmillan Company, New York, 1934.

Social and biological significance of changing birth rates in the United States.

WHO SHALL SURVIVE?, *by* J. L. Moreno. Pages 400, 100 colored charts, price $4.00. Nervous and Mental Disease Publishing Co., Washington, D. C., 1934.

Not what the title would imply: but a study of emotio-intellectual reactions of individuals with other individuals and with groups.

THE POPULATION PROBLEM IN INDIA, *by* P. K. Wattal. Price Rs. 3-8. Bennett, Coleman & Co., 1934.

Vital statistics, etc., from a region of the globe where Malthus' checks on population are said to apply.

CHARLES DARWIN'S DIARY

Verbatim reproduction of Darwin's notes made during the "Beagle" voyage give a new and vivid picture of his thoughts and observations during the years when the theory of Natural Selection was beginning to take form.

DARWIN himself published two editions of his diary with the suppression of such passages as he thought would be undignified in cold print or likely to give offense, and with the addition of the mature conclusions which he had reached concerning the significance of his observations after several years of reflection and study. The present "Diary" is a verbatim reproduction from Darwin's original notebooks (misspellings and all) of what he wrote from day to day during the voyage.* It has less value than Darwin's own publication of his diary as an exposition of his views on evolution, but it gives us a better picture of the man as he metamorphosed from the guileless youth who left England in 1831 to the philosophic naturalist who returned in 1836.

This period in English history was one of expansion, material and intellectual. The voyage of the "Beagle" was only one of numerous expeditions sent out by the British government to explore and chart the coasts and harbors of little known and unexploited lands in the interest of British commerce. Darwin was taken along as "naturalist" on the recommendation of two Cambridge University professors who had found him to be a thoughtful and observing youth. Their confidence in him was fully justified.

The Voyage Begins

Here are some of his first impressions of life on shipboard:

November 22nd. Went on board & returned in a panic on the old subject, want of room. Returned to the vessel with Cap. FitzRoy, who is such an effectual & good-natured contriver that the very drawers enlarge on his appearance & all difficulties smooth away.

23rd. This has been a very important day in the annals of the Beagle; at one o'clock she was loosed from the moorings & sailed about a mile to Barnett pool. Here she will remain till the day of sailing arrives. This little sail was to me very interesting, everything so new & different to what one has ever seen, the Coxswain's piping, the manning the yards, the men working at the hawsers to the sound of a fife; but nothing is so striking as the rapidity & decision of the orders & the alertness with which they are obeyed. There remains very little to be done to make all ready for sailing. All the stores are completed & yesterday between 5 & 6 thousands canisters of preserved meat were stowed away. Not one inch of room is lost, the hold would contain scarcely another bag of bread. My notions of the inside of a ship were about as indefinite as those of some men on the inside of a man, viz., a large cavity containing air, water & food mingled in hopeless confusion.

24th. A very fine day & an excellent one for obtaining sights. Every body hailed the sun with joy, for untill the time is well taken, we cannot leave harbour. I went on board several times in the course of the day; but did not succeed in doing any good, as they were changing the place of anchorage & that is not the time for a Landsman to give trouble about his own lumber.

November 25th. Very busily employed on board in stowing away my clothes & after

**Charles Darwin's Diary of the Voyage of H. M. S. "Beagle,"* edited from the manuscript by Nora Barlow. $6.50. The Macmillan Co., New York, 1933.

that in arranging the books, did not leave the vessel till it was dark.

His plans and ambitions are outlined thus:

December 13. An idle day; dined for the first time in Captain's cabin & felt quite at home. Of all the luxuries the Captain has given me, none will be so essential as that of having my meals with him. I am often afraid I shall be quite overwhelmed with the number of subjects which I ought to take into hand. It is difficult to mark out any plan & without method on shipboard I am sure little will be done. The principal objects are 1st, collecting, observing & reading in all branches of Natural history that I possibly can manage. Observations in Meteorology, French & Spanish, Mathematics, & a little Classics, perhaps not more than Greek Testament on Sundays. I hope generally to have some one English book in hand for my amusement, exclusive of the above mentioned branches. If I have not energy enough to make myself steadily industrious during the voyage, how great & uncommon an opportunity of improving myself shall I throw away. May this never for one moment escape my mind & then perhaps I may have the same opportunity of drilling my mind that I threw away whilst at Cambridge.

Wind and weather bring disappointments.

December 15th. The wind continues in the old point S. W., which independently of detaining us appears invariably to bring bad (weather) with it. The ship is full of grumblers & growlers, & I with sea-sickness staring me in the face am as bad as the worst. The time however passes away very pleasantly, but instead of working, the whole day is lost between arranging all my nick-nackiries & reading a little of Basil Hall's fragments.

16th. This day is come to its close much in same way as yesterday. I am now sitting in my own corner feeling most comfortably at home. This is the first time that I have not left the vessel during the whole day. The wind with torrents of rain is sweeping down upon us in heavy gusts.

Looking on the bright side.

December 23rd. In the morning Sullivan, Bynoe & myself shot matches with the rifle for sundry bottles of wine to be paid for & drunk at the Madeira islands. In the evening went with Stokes to a bad concert. Although I am continually lamenting in the bitterness of my heart against all the long delays & vexations that we have endured, I really believe they have been much to my advantage, for I have thus become broken in to sea habits, without having at the same time to combat with the miseries of sickness.

Reflecting, as always, on why things are as they are.

December 25th. Christmas day, in morning went to Church & found preaching there an old Cambridge friend, Hoare. Dined at 4 o'clock with Gun-room officers. It does me good occasionally dining there, for it makes me properly grateful for my good luck in living with the *Captain*. The officers are all good friends. Yet there is a want of intimacy, owing I suppose to gradation of rank, which much destroys all pleasure in their society. The probability of quarrelling & the misery on ship board consequent on it produces an effect contrary to what one would suppose; instead of each one endeavouring to encourage habits of friendship, it seems a generally received maxim that the best friends soon turn out the greatest enemies. It is a wonder to me, that this independence one from another, which is so essential a part of a sailor's character, does not produce extreme selfishness. I do not think it has this effect, & very likely answers their end in lessening the number of quarrels, which always must necessarily arise in men so closely united. Let the cause be what it may, it is quite surprising that the conversation of active intelligent men who have seen so much & whose characters are so early & decidedly brought out, should be so entirely devoid of interest.

Christmas day is one of great importance to the men: the whole of it has been given up to revelry, at present there is not a sober man in the ship: King is obliged to perform duty of sentry, the last sentinel came staggering below declaring he would no longer stand on duty, whereupon he is now in irons getting sober as fast as he can. Wherever they may be, they claim Christmas day for them-

selves, & this they exclusively give up to drunkedness, that sole & never failing pleasure to which a sailor always looks forward to.

Monday, December 26th. A beautiful day, & an excellent one for sailing, the opportunity has been lost owing to the drunkedness & absence of nearly the whole crew. The ship has been all day in state of anarchy. One day's holiday has caused all this mischief such a scene proves how absolutely necessary strict discipline is amongst such thoughtless beings as Sailors. Several have paid the penalty for insolence, by sitting for eight or nine hours in heavy chains. Whilst in this state, their conduct was like children, abusing every body & thing but themselves & the next moment nearly crying. It is an unfortunate beginning, being obliged so early to punish so many of our best men; there was however no choice left as to the necessity of doing it. Dined in gun-room & had a pleasant evening.

Off at last.

December 27th. I am now on the 5th of Jan. writing the memoranda of my misery for the last week. A beautiful day, accompanied by the long wished for E. wind. Weighed anchor at 11 o'clock & with difficulty tacked out. The Commissioner Cap. Ross sailed with us in his Yatch. The Capt. Sullivan & myself took a farewell luncheon on mutton chops & champagne, which may I hope excuse the total absence of sentiment which I experienced on leaving England. We joined the Beagle about 2 o'clock outside the Breakwater, & immediately with every sail filled by a light breeze, we scudded away at the rate of 7 or 8 knots an hour. I was not sick that evening but went to bed early.

28th. Waked in the morning with an eight knot per hour wind, & soon became sick & remained so during the whole day. My thoughts most unpleasantly occupied with the flogging of several men for offences brought on by the indulgence granted them on Christmas day. I am doubtful whether this makes their crime (of) drunkedness & consequent insolence more or less excusable.

Lack of space forbids our sharing further his experiences in viewing tropical life for the first time at the Canary Islands, examining the rich contents of the tow net, as they sailed leisurely on, crossing the equator and finding himself at last in the Southern Hemisphere, yet not more uncomfortable than on "a hot summer's day in England."

The Tropics

On reaching Brazil he goes ashore in a New World.

February 29th. The day has passed delightfully: delight is however a weak term for such transports of pleasure: I have been wandering by myself in a Brazilian forest: amongst the multitude it is hard to say what set of objects is most striking; the general luxuriance of the vegetation bears the victory, the elegance of the grasses, the novelty of the parasitical plants, the beauty of the flowers, the glossy green of the foliage, all tend to this end. A most paradoxical mixture of sound & silence pervades the shady parts of the wood: the noise from the insects is so loud that in the evening it can be heard even in a vessel anchored several hundred yards from the shore: yet within the recesses of the forest a universal stillness appears to reign. To a person fond of Natural history such a day as this brings with it pleasure more acute than he ever may again experience. After wandering about for some hours, I returned to the landing place. Before reaching it I was overtaken by a Tropical storm. I tried to find shelter under a tree so thick that it would never have been penetrated by common English rain, yet here in a couple of minutes, a little torrent flowed down the trunk. It is to this violence we must attribute the verdure in the bottom of the wood: if the showers were like those of a colder clime, the moisture would be absorbed or evaporated before reaching the ground.

March 1st. I can only add raptures to the former raptures. I walked with the two Mids a few miles into the interior. The country is composed of small hills & each new valley is more beautiful than the last. I collected a great number of brilliantly coloured flowers, enough to make a florist go wild. Brazilian scenery is nothing more nor less than a view in the Arabian Nights, with the advantage of reality. The air is deli-

ciously cool & soft full of enjoyment one fervently desires to live in retirement in this new & grander world.

A month later they go on to Rio de Janeiro, and then to Montevideo. He makes several excursions on land, studying the geology, the plants, the animals, and the people. The political instability and unrest are scarcely understandable to one accustomed to the orderly civilization of England. Of slavery he distinctly disapproves, differing therein from Capt. FitzRoy, their close friendship being strained at times when the subject is discussed.

They go on to Patagonia, where the weather is less agreeable.

December 11th. The Barometer had given good warning of a change of weather; it is the anniversary of our first attempt to get out of the English channel, & as on that day we were met by a heavy breeze from the S. W. With me the association was perfect though not very satisfactory, between the two days: my stomach plainly declared it was of terrestrial origin & did not like the sea.

The first eventful year thus came to a close. Four more were to follow, likewise combining danger and hardship with delightful novel experiences and adventures. They tried in vain to round Cape Horn, being turned back by tempestuous weather, but two years later passed safely through Magellan's Strait, having meantime explored Patagonia, Tierra del Fuego, and the Falkland Islands.

Darwin's interest in geology and his knowledge of it had meanwhile increased greatly. He notes the occurrence of the bones of extinct sloths and armadillos of gigantic size in the horizontal strata of the pampas, the occurrence of marine shells remote from the sea and infers recent elevation of the land.

Visit to the Galápagos Islands

In June, 1834, they entered the Pacific, exploring and surveying the coast and larger islands of Chili and thence north to Peru. A severe earthquake was experienced and its disastrous effects vividly described. An expedition was made inland across the Andes and return. Everywhere interest was divided between geology of the country and its life, plant, animal, and human. Nothing seems to have escaped his observation, and nothing failed to interest him.

From Lima the "Beagle" sailed to the Galápagos Islands in September, 1835. The survey of these islands is perhaps the best known incident of the entire voyage, because it was here, from comparing the fauna of one island with that of another and the fauna of all with that of South America, that the idea of evolution first came clearly into Darwin's mind. Captain FitzRoy, Darwin's senior and close associate during the long voyage, was an ardent creationist and profoundly disapproved of Darwin's later advocacy of natural selection. This may possibly have delayed the publication of Darwin's evolutionary conclusions.

From the Galápagos the voyage continued to Tahiti, New Zealand, Australia, and South Africa, and thence across the Atlantic via St. Helena to Bahia, Brazil, once more, and home by the Azores to Falmouth, England, in October, 1836.

Darwin's soul had run the gamut of emotion in his five-year voyage and may, he fears, have grown callous.

October 2nd. After a tolerably short passage, but with some very heavy weather, we came to an anchor at Falmouth. To my surprise & shame I confess the first sight of the shores of England inspired me with no warmer feelings, than if it had been a miserable Portugeese settlement. The same night (& a dreadfully stormy one it was) I started by the Mail for Shrewsbury.

Views Regarding North Americans

North Americans can not fail to be interested in the few passages in the diary which refer to them.

Under October 12th-16th, 1835, we find this entry, made at the Galápagos Islands:

We all were busily employed during these days in collecting all sorts of Specimens. The little well from which our water was procured was very close to the Beach: a long Swell from the Northward having set in, the surf broke over & spoiled the fresh water. We should have been distressed if an American Whaler had not very kindly given us three casks of water (& made us a present of a bucket of Onions). Several times during the Voyage Americans have showed themselves at least as obliging, if not more so, than any of our Countrymen would have been. Their liberality moreover has always been offered in the most hearty manner. If their prejudices against the English are as strong as ours against the Americans, they forget & smother them in an admirable manner."

Again, in commenting on social conditions in New South Wales, he says, p. 387:

I am not aware that the tone of Society has yet assumed any peculiar character; but with such habits & without intellectual pursuits, it can hardly fail to deteriorate (& become like that of the people of the United States).

The part in parentheses had been crossed out by Darwin, as if, after all, there might be doubt of its correctness.

Evidence of British self-satisfaction, or perhaps merely homesickness, is expressed in this entry made at Tahiti, Nov. 17th, 1835.

The pineapples here are also of such excellence, as to be better than those reared in England, & this I believe to be the last & highest compliment which can be paid to a fruit or indeed anything else.

Longing for home again finds expression on December 19th, 1835, as they near New Zealand.

The Meridian of the Antipodes is likewise passed; every league, thanks to our good fortune, which we now travel onwards, is one league nearer to England.

His feelings, on leaving Australia, are much like those which a Bostonian or a Philadelphian might express toward Chicago.

Farewell Australia, you are a rising infant & doubtless some day will reign a great princess in the South; but you are too great & ambitious for affection, yet not great enough for respect; I leave your shores without sorrow or regret.

On leaving Mauritius, he makes this entry:

May 9th. In the evening we sailed from Port Louis on our way to the Cape of Good Hope; since leaving England I have not spent so idle & dissipated a time. I dined out almost every day in the week: all would have been very delightful, if it had been possible to have banished the remembrance of England. Pleasant as the society appeared to us, it was manifest even during our short visit that no small portion of jealousy, envy & hatred was common here, as in most other small societies. Alas, there does not exist a terrestrial paradise where such feelings have not found an entrance.

The editor of this volume says truthfully in her preface:

After the lapse of one hundred years I believe it is right to assume that this exact transcript of my grandfather's original Journal can now claim to rank not only as a scientific historical document, but also as a book that can hold its own on the strength of its spontaneity and charm. To many readers Charles Darwin stands as a figure far advanced both in knowledge and in years; this volume contains a picture of him in the first freshness and eager enjoyment of life.

W. E. Castle
Bussey Institution, Harvard University

AN INHERITED "HOLLOW CHEST"

Koilosternia, a New Character Dependent upon a Dominant Autosomal Gene*

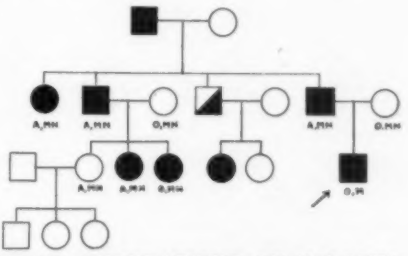
LAURENCE H. SNYDER and GEORGE M. CURTIS
Ohio State University

DURING the progress of a course in genetics at the Ohio State University, a student presented himself with a peculiar chest anomaly. This deformity, to be described in detail later, consisted of a pronounced depression in the chest, much as though a ball had been pressed in and withdrawn, leaving the hollow. The anomaly was known to have appeared in eight members of the family, and was generally transmitted directly from parent to offspring.

In Figure 9 is shown the pedigree of the family. It will be noted that of the eight affected members, four are males and four females. There is no evidence of sex-linked or sex-influenced transmission. In one instance an affected daughter had parents free from the anomaly. The father in this case, however, had an extremely flat chest.

The evidence points to a dominant autosomal gene as the basis of the character. Under certain environmental or possibly genetic conditions, however, the anomaly may fail to reach full expression.

Blood groups and *M-N* reactions were determined for all the members whom it was possible to reach. The results are given in Figure 9. The new gene does not appear to be linked with the factors for the *A-B* blood groups, but might be linked with the gene for antigen *M*. There are not enough individuals available to settle this point. The entire family consisted of tasters for phenyl-thio-carbamide, so that linkage data for the taste genes cannot be had.



THREE GENERATIONS OF HOLLOW CHEST

Figure 9

Pedigree of koilosternia, a newly described character in man dependent upon a dominant autosomal gene. Affected individuals are shown in black. The half-black symbol indicates an extremely flat chest, but no depression. The letters beneath the symbols show the blood group and *M-N* antigen grouping of the individual.

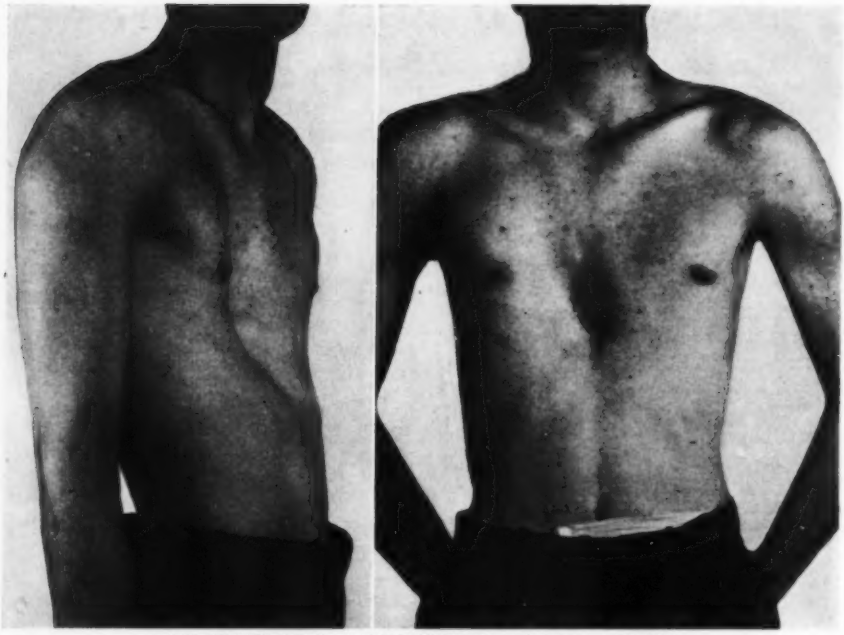
Description of "Hollow Chest"

As far as we are aware, this anomaly is previously undescribed. We have named it koilosternia, from the Greek words *koilos*, hollow, and *sternon*, chest. Since all affected individuals in the pedigree are presumably heterozygous, we have no means of knowing what the character would be in homozygous form.

In order to discover if possible the mode of action of the gene in producing the finished character, the patient was hospitalized and subjected to a complete clinical and laboratory investigation. The hospital report follows:

R. H., No. 342222, a male student of 19, entered the University Hospital May 4th, 1934, for investigation of a congenital deformity of the chest. There were no other complaints, and no symptoms whatever referable to the deformity.

*"Studies in Human Inheritance XI" from the Departments of Zoology and Medical Research, Ohio State University.



AN INHERITED DEPRESSION OF THE CHEST

Figure 10

Side and front views of chest of propositus (Figure 9), showing position and extent of the deformity. That such a peculiar deviation from the normal should be inherited would seem to be highly improbable, but the evidence that this has been the case for three generations can leave no doubt as to this particular instance.

His past history was negative so far as the deformity was concerned. He had indulged in all activities and in various sports since boyhood without any noticeable incapacitation. Three years ago he fractured two lower ribs on the opposite side. These healed uneventfully, and without sequellae. Examination by systems revealed no abnormalities. He was a healthy, normal, active student.

The family history has already been discussed. Physical examination revealed a well developed, well nourished, ambulatory male, with a pronounced chest deformity, but otherwise in excellent health.

There was an oblique bony ridge, about 4 cm. in length, just above the left supra orbital ridge. The teeth were in good condition. The head was otherwise negative. The neck was normal. The thyroid was normal. The pulse was 80, and was regular and of good force. The blood pressure was 126/78.

Save for the deformity, which will be described, the chest was normal. The heart and lungs were negative. The abdomen, extremities and genitalia revealed no abnormalities upon careful examination. The reflexes were normal.

There was an unusual deformity of the chest in the region of the right lower sternum (Figure 10). This was essentially a trough-shaped depression, measuring about 15 cm. vertically, 10 cm. horizontally, and being about 5 cm. deep. It began above at the level of the fourth costal cartilage and extended below the seventh costal cartilage. Its greatest portion was to the right of the midline. The xiphoid process and the lower body of the sternum were forced over to the left, so that their anterior surfaces faced to the right. The left costal margin was consequently more prominent than the right. The right upper chest was flatter than the left. Respiratory movements appeared to be symmetrical. There was no lagging of the deformed right chest.

Palpation revealed an acute angulation of ribs 2 to 8, inclusive, in the mid-clavicular

line. The manubrium of the sternum was slightly tilted to the right. No abnormalities were detected in either lung.

Laboratory investigation revealed that the urine was normal. The blood was normal. Both the erythrocytes and hemoglobin were high. There were 7,200 leucocytes, and the differential count was within normal range. The Wassermann and Kahn tests were negative.

The basal metabolic rate was plus 11, with the pulse 65, the temperature 98.8, the respirations 10, and the blood pressure 114/74 in the basal state. The vital capacity was 3,745 cc. The blood calcium and phosphorus were normal. The blood iodine was normal. There was, thus, no evidence of disturbed thyroid or parathyroid function. During the three days of hospital investigation the pulse, temperature and respirations were normal.

X-rays reveal the deformity. However, no bone abnormality is discernible, save the deformity. Likewise no other abnormalities are evident in either chest. The heart position is obviously in correspondence with the depressed right chest.

Thus the congenital depression deformity of the lower right chest is the single outstanding abnormality. The other findings reveal a healthy normal individual without any evidence of impairment. There is no discernible evidence pointing to the cause of the deformity, other than that it is apparently dependent upon a dominant autosomal genetic factor.

The Background of Our Cultivated Plants

THIS is an interesting and instructive book* written in a vocabulary easily comprehensive to the average lay reader. It contains brief and general discussions of the common crop plants grown in the United States, some of the better known ornamentals and a few of the tropical plants whose products are used commonly in the household or are otherwise of exceptional interest. In all, approximately 140 plants are treated. In most cases a brief description is given of the plant, the history of its agricultural development, its distribution over the earth's surface, the conditions under which it grows and its use to man.

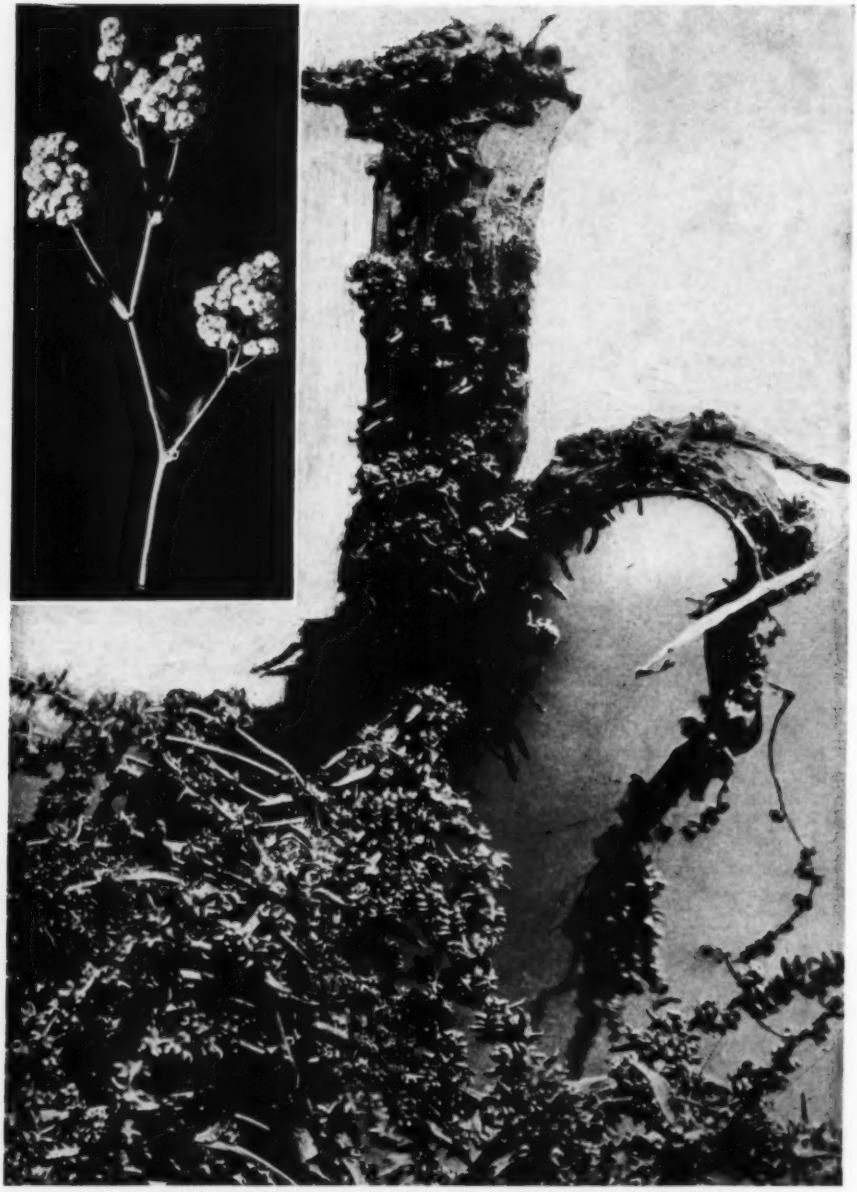
The book is composed of twenty-four chapters. The first two chapters are introductory in nature, having to do with the origin of cultivated plants and the classification of plants. There are six chapters devoted to general topics, such as, ornamental plants, table fruits and nuts, spices and tropical fruits, medical plants, etc. The remaining sixteen chapters carry the reader through the plant kingdom in natural order by families of plants. In each family are discussed the most outstanding economic plants belonging to it. Generally speaking, the plants of most importance in our every day life are given the most space.

The authors have written the book with the intention that it may serve as a supplement to the necessarily more technical text books of botany. It fulfills this intention and also serves as a ready reference to anyone interested in the background of our cultivated plants. We do not feel that it is sufficiently detailed to serve as a text book of economic botany but believe it admirably suited as a source of ready information for teachers wishing to implant the dry facts of science in a matrix of human interest.

The book is well illustrated and the figures well chosen, except the maps showing distribution, which leave much to be desired in their execution. There are a few general statements with which we could take exception, but they are of minor importance in the work as a whole and are hardly avoidable in a work of such a general character.

C. O. Erlanson
U. S. Department of Agriculture.

*Robbins, Wilfred William, and Francis Ramaley. *Plants Useful to Man.* P. Blackiston's Son and Co., 1933.



ABNORMALITIES OF ALFALFA AND SUGAR BEET

Figure 11

The small insert at the left shows a vegetative proliferation replacing alfalfa blossoms. This abnormality is extremely rare in the field but was reproduced abundantly by inbreeding, giving strong evidence of its inherited character. The proliferated branch of sugar beet, occupying the rest of the illustration, represents another abnormality whose incidence was enormously increased by inbreeding.

ABNORMALITIES IN INBRED ALFALFA AND SUGAR-BEETS

GEORGE STEWART*
U. S. Forest Service, Ogden, Utah

THE writer has observed four times in his life, twice during 10 years of alfalfa-growing and twice during 15 years of scientific work, a peculiar vegetative proliferation which replaces the blossoms of alfalfa. Probably hundreds of millions of alfalfa plants have been observed since the abnormality was first noted, and only three other cases have appeared. A friend has seen three or four such cases, once several in an area of a few square rods. While perhaps not as scarce as the figures indicate, this abnormality is extremely rare under field conditions.

The plant last observed was found while inspecting an 80-acre seed field for weed contamination in Millard County, Utah. It was marked and seed from it later harvested for the writer by the owner of the field. The seeds were few in number and failed to germinate on wet blotters in the laboratory. When seeded in the field a few plants grew and one showed the same abnormality; four or five others were normal. The abnormal plant was bagged for inbred seed and the seeds obtained sown in a row from which 40 plants were grown. Of these, on nine plants the vegetative proliferation so completely replaced the petals of the flowers as to make identification of their color impossible; on six other plants were found a few normal blossoms which permitted color identification but with nearly all petals replaced by the proliferation.

This abnormality was reproduced in plots in five or six plants by open-fertilization and in 15 out of 40 plants after one generation of inbreeding, thousands of times, perhaps millions of times, more frequently than in the field.

The nature of the proliferation is shown in Figure 11. Instead of blossoms there was a mealy wart-like mass, white in color and resembling somewhat the flower buds of seed onions just before the flowers open.

Abnormality in Sugar-beet Branching

A broad belt-like proliferation of a branch on a sugar-beet plant was observed to occur for three successive generations in one partially inbred sugar-beet stock. No opportunity was found to make a further study of its inheritance. It was not observed in any other of more than 400 lines of beets under observation.

The nature of the proliferation is shown by comparing the proliferated branch with a normal top branch in Figure 11.

◆

Large Families in Hungary

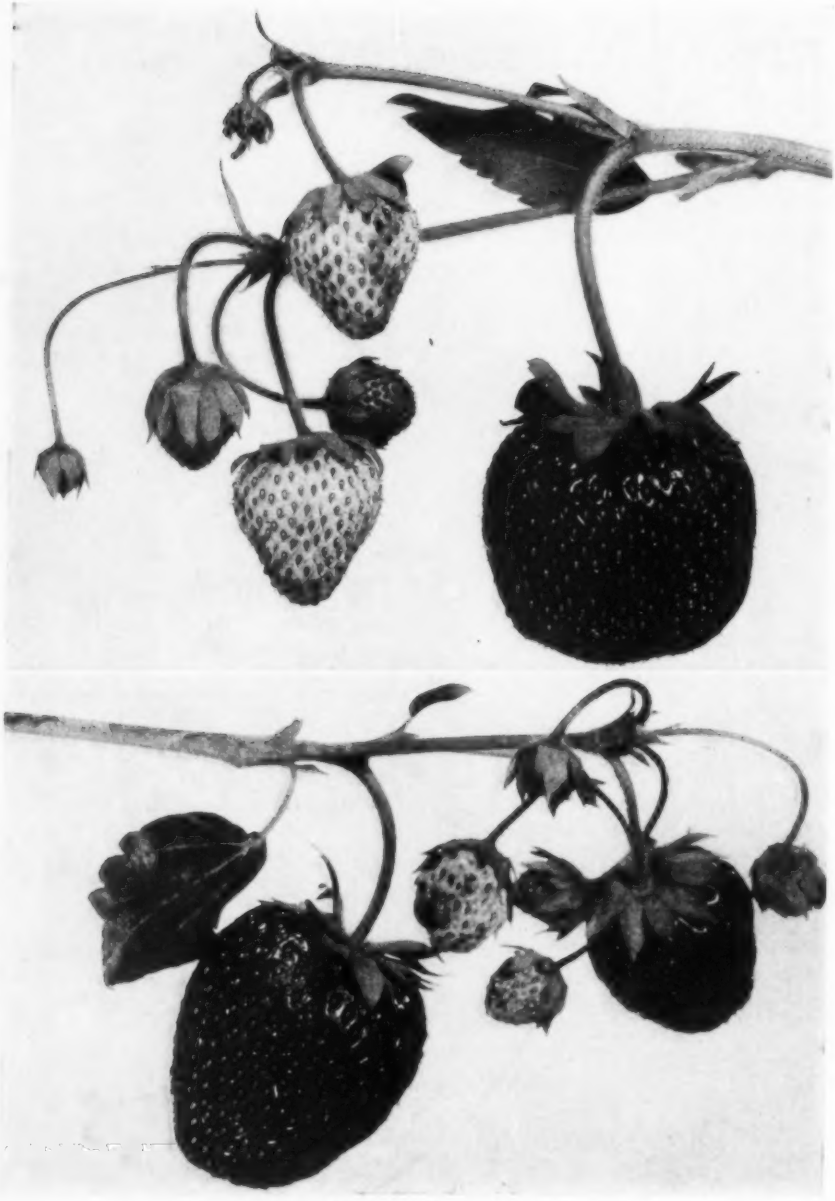
BUDAPEST, August 23.—Mrs. Antal Krammer, a peasant woman living near Budapest, yesterday was awarded the government's first prize for having more children than any other mother in Hungary.

Mrs. Krammer, who is only 48 years old, now has 21 children. She was married at 16.

Gold medals were awarded 6,000 other Hungarian mothers, who, combined, have a total of 80,000 children—an average of 13 1/3 children each.

This is proof, said Hungarian authorities, that Hungarian parents are the most prolific in the world.—*By the Associated Press.*

*Former Station Agronomist, Utah Agricultural Experiment Station. Publication authorized by Director. Acknowledgment is here made to J. W. Carlson for help on the alfalfa and to Wesley Keller for help on the sugar-beets.



TWO NEW VARIETIES

Figure 12

The Fairfax (above) and the Dorsett (below) are two of the seven varieties which have resulted from the breeding work of the U. S. Department of Agriculture. These two varieties are general-purpose dessert berries adapted to the Middle Atlantic States and to Southern New England States.

TWELVE YEARS OF STRAWBERRY BREEDING

II—From 170,000 Seedlings, Seven Named Varieties: A Summary of the Crosses Made and An Evaluation of Their Effectiveness as Breeding Material

G. M. Darrow, G. F. Waldo, C. E. Schuster, and B. S. Pickett

THE strawberry breeding work of the United States Department of Agriculture was begun as a separate project in 1920 in Maryland, and since then it has been extended to cooperative work with the North Carolina Department of Agriculture at Willard, N. C., and with the Oregon Agricultural Experiment Station at Corvallis, Ore.

The first article in this series[2] discussed the technique of strawberry breeding, and the major objectives of the project in which the authors have been engaged. In this article it is proposed to discuss the methods we have used in attempting to rearrange desirable genes to get as many as possible into a single variety. In general five types of crosses have been made in carrying on this work: (1) Crosses may be made between varieties that succeed in the district which the work is intended to benefit. The origination of the Corvallis variety by one of the authors (C. E. S.) at the Oregon Agricultural Experiment Station, by crossing two varieties grown in Oregon is an example of successful breeding using this method. (2) Varieties that succeed in a district may be crossed with important varieties of other districts or countries. The Blakemore and Dorsett are examples of such crosses resulting from the work of the United States Department of Agriculture. (3) Crosses may be made with wild species which have some desirable characteristics not found in cultivated varieties. Both the Ettersburg 121, originated by A. F. Etter in California, and the varieties originated at the Alaska Experiment Station resulted from crossing horticultural varieties and wild species. (4) Varieties possessing desirable characteristics to a marked degree may be selfed and the selected seedlings may be used in further inbreeding to accentuate definite desirable qualities. (5) Combinations of the above methods may be used. Varieties that succeed in a district have necessarily many qualities which adapt them to that particular climate and the market requirements of that region. The attempt to combine these qualities in one variety is the logical approach of the breeder. No desirable varieties have as yet resulted from direct inbreeding, although this method has not yet been fully tried. Inbreeding with later outbreeding, or crossing of highly inbred lines, may prove of value. Certain crosses may also give mutations, or at least unusual results, and may be important. Thus the Rockhill variety which resulted from a cross made by Harlow Rockhill between Progressive and Early Jersey Giant represents a new type. Different seedlings of U. S. D. A. 652* × Blakemore have fruit flavors under certain weather conditions ranging from strawberry to raspberry, banana, apple, and grape. Their value is not yet proven, but the range of variation which may be selected from by the breeder is greatly increased.

History of the Breeding Experiments

About one-half acre of seedlings resulting from the 1920 crosses bore fruit at Glenn Dale, Maryland, in 1922. Included among these were rows of open pollinated seedlings of several standard varieties, the seed having been derived

*For the parentage of the U. S. D. A. numbers in this article, see Table I, Page 452.

from plants of many standard varieties grown in adjacent rows. The fruit of those from hermaphrodite varieties was generally inferior but the foliage resembled that of the parents, the plants being smaller and weaker, and the fruit in general undesirable. The seedlings of the Aroma, Kelko, Lupton, Stevens Late, and Tennessee were apparently all self-pollinated. A few seedlings of the Trebla seemed to be crosses, being much more vigorous than the other Trebla seedlings. All seedlings of two pistillate varieties, *Fragaria virginiana* No. 27, and Sample, were necessarily crosses and were far more vigorous and productive than most of the seedlings from the hermaphrodite forms. Plants of a wide range of crosses fruiting at the same time were also very vigorous.

From this simple test the following conclusions were reached: that most perfect-flowered varieties are self-pollinated; self-pollinated seedlings are generally weaker than their parents; and carefully planned breeding would result in far more vigorous seedlings than sowing uncrossed seed of hermaphrodite types. This test also confirmed conclusions that American varieties as compared with European were more uniform in plant and fruit characteristics. These conclusions were reached as the result (1) of a review of the history of the cultivated strawberry, and (2) of observations on European varieties and on those originated by Mr. A. F. Etter. European strawberries as grown in collections in this country represent a much greater range of forms in both plant and leaf characteristics than do standard American varieties even though descended from the same species. Louis Gauthier and La Constante resemble *Fragaria chiloensis* in many respects, while Royal Sovereign resembles it more than most American varieties. A very different European type is represented by Avant Coutet which resembles and may be identical with the American variety Excelsior. Its leaves and fruit are very like *F. virginiana*, the wild strawberry of eastern North America.* It should be noted that European varieties have all been produced by crossing and selection deliberately undertaken by breeders. There are no wild species in Europe which cross, at least readily, with garden varieties. Mr. Etter's strawberries are

TABLE I.—Parentage of U.S.D.A. Selections Referred to by Number in the Text.

No. 25 = Van Fleet 3 × Campbell
No. 27 = Euresko × Chesapeake
No. 542 = Unknown
No. 624 = Royal Sovereign × Howard 17
No. 631 = Portia × Euresko
No. 652 = Red Sugar × Howard 17
No. 668 = Parsons × Ettersburg 450
No. 682 = Howard 25 × Royal Sovereign
No. 694 = Progressive × *Fragaria chiloensis* (Chilean)
No. 778 = Missionary × Howard 17
No. 817 = Howard 25 × Ettersburg 80
No. 822 = Unknown
No. 842 = Howard 25 × Ettersburg 121
No. 844 = Howard 25 × Ettersburg 121
No. 874 = Howard 25 × Ettersburg 121

*Thickness of leaves best illustrates one of the important differences between European and American varieties. In one set of measurements of the thickness of leaves of strawberry species as grown under Maryland conditions, the following record was obtained:

TABLE II.—Thickness of 30 Leaflets.

Species	Thickness Cm
Fragaria Chiloensis 5-A	1.05
F. chiloensis 5-C	1.13
F. cuneifolia No. 14	.84
F. moschata (M. Hautbois)	.77
F. virginiana No. 27	.87[a]
F. chiloensis 5-C × U.S.D.A. 613 (.90 to 1.15 av.)	1.00[b]
F. cuneifolia × U.S.D.A. 542 (.67 to .81 av.)	.74[b]

[a] Other selections of *F. virginiana* measured at another season had thinner leaves than this selection.
[b] 30 leaflets of 10 different seedlings averaged.

The thickness of the leaves of *F. chiloensis* is about 20 per cent greater than that of *F. virginiana* when measured in this way under Maryland conditions. Measurements of several American varieties gave no significant differences in thickness, but European varieties showed a variation of 38 per cent, even greater than the selections of species used. American varieties had a thickness about like that of *F. virginiana* while European sorts ranged from that of *F. virginiana* to that of *F. chiloensis*. (In some studies in Oregon the average diameter of 10 leaflets gave 54 per cent greater diameter for leaves of *F. chiloensis* than for *F. virginiana* No. 27.

chiefly if not entirely crosses of garden varieties with selections of *F. chiloensis* or descendants of such crosses. They also show a great range of types though few of them resemble *F. virginiana* as much as Avant Coutet.

In contrast most American varieties are represented by the Dunlap, Klondike, and Missionary type with the Chesapeake, Marshall and Howard 17 (*Premier*) varieties as the more divergent forms. None, however, approaches *F. chiloensis* at all closely. The history of eastern American strawberries indicates that they have evolved from a few earlier varieties with little or no recent admixture of *F. chiloensis* or of varieties from Europe. Their plant and fruit characteristics seem to have approached closer and closer through the years to the wild *F. virginiana* of the Atlantic Coast region. Many of those American varieties of which Missionary and Gandy are examples, were found in the wild. They were probably seedlings, the result of a cross between wild and cultivated varieties. In fact, the wild strawberries in many sections are now all, or almost all, descended from the native strawberry crossed with cultivated varieties. The selections of breeders also show many characteristics found in the native strawberries. Thus the cultivated berry in America is in general a product more uniform than that of Europe and at the same time much more closely related to the strawberries to be found growing wild in the eastern United States.

This evolution during the past hundred years has resulted in garden strawberries well adapted in plant characteristics to eastern American conditions. They grow and produce runners freely in the humid regions of eastern United States and as compared to varieties of western United States and Europe are relatively resistant to leaf and root diseases. Their berries, however, have less flavor under some conditions and are softer, with less range in texture, than some of the European varieties and those originated by Mr. Etter. Apparently through the years some characters have been lost or neglected in the development of the American strawberry. Cultivated varieties of the eastern United States show, therefore, less divergent types and, as the test of growing has demonstrated, the selfed seedlings are less vigorous than their parents, while outbreeding resulted in a more vigorous F_1 generation.

Before the Federal breeding work was started, Fletcher[3] had already concluded that the cultivated strawberry was derived wholly or almost wholly from *Fragaria virginiana* crossed with *F. chiloensis*, and Valleau[5] had called attention to the sex types of the wild *F. virginiana*. Dr. Walter Van Fleet (who was associated with our experiments as an adviser from 1920 until his death in January, 1922) had used European strawberries in his earlier breeding experiments from which he obtained the Early Jersey Giant and the John Cook. W. F. Wight had made a collection of several species and some varieties which were available for the breeding work. A survey had been made of American varieties and production methods during the years before the war (1913-1916). Greater advances with the strawberry seemed possible by breeding than in any other line of research. Therefore in the years since 1920 breeding work has been emphasized. Many research problems growing out of the breeding work have been investigated but the improvement of varieties has remained the central problem.

Materials

Systematic collections of varieties and species since 1920 have added greatly to the effectiveness of the breeding work. Scores of varieties and many collections of species have been introduced from foreign countries through the Division of Foreign Plant Introduction. About 75 collections of plants of native strawberries were obtained, through the kindness of W. A. Dayton of the Forest Service, from forest rang-

ers in the western United States. Many collections were made on the beaches of Oregon by the writers while many institutions and individuals have kindly sent in collections.

In all, over 130 varieties and 20 selections of species have actually been used in the breeding. Forty-four of the varieties used were of European origin, some were American and 54 were selections from our own crosses. Selections of the three species, *Fragaria chiloensis, F. cuneifolia,* and *F. virginiana,* have been the principal species types used.

In the earlier breeding work named varieties were used almost entirely. Thus 126 different crosses were represented in the seedlings from which the selection of 1925 were made. None of these was a cross of previous selections. However, seven years later, out 113 different crosses fruited in 1932 in Maryland, 11 were between varieties, 47 were between varieties and selections, and 55 were between different selections. Of the seedlings selected as promising in 1932 in Maryland, only five were crosses between varieties, 92 were crosses between varieties and previous selections, and 59 were crosses between previous selections. For fruiting in 1933, there were 17 crosses between varieties, 55 between varieties and selections, and 41 between selections. Many of the characteristics considered desirable are now in selections, some of which are saved because they combine many desirable characteristics even though they are so lacking in some one important characteristic that they are of no direct value.

Results

The number of selections, and the year in which they were made, is given in Table III.

Several explanations should be made concerning this table. In the first place, the numbers of seedlings which were fruited in the field represent but a small part of the total number of seedlings raised. In the seed flats many thousands have been lost by damping-off and by other fungus infections. There was one instance of sulfur injury. In 1928 some 15,000 seedlings were lost as the result of a cyclamen mite infestation. In that year also a severe rain storm washed away or buried several thousand seedlings. In 1930 the drought and in 1931 the root aphid killed out thousands of seedlings. In 1931, soil, water, drought, white grub and root rot damage also killed many thousands. In some instances the weaker or more susceptible seedlings have been the first to be eliminated, so that the losses have selective value. Tens of thousands, however, have been lost without regard to their probable value.

TABLE III.—Approximate number of strawberry seedlings fruited and number of selections made at the Maryland, Oregon, and North Carolina stations and number still left Nov. 1, 1932, in strawberry breeding work at the Maryland station.

Year	Glenn Dale, Md.			Corvallis, Ore.		Willard, N. C.	
	Approx. No. seedlings	Number of selections	Number left	Number seedlings	Number selections	Number seedlings	Number selections
1922	1,800	100	10	----	----	----	----
1923	3,500	175	17	----	----	----	----
1924	unknown	124	4	----	----	----	----
1925	7,989	380	100	----	----	----	----
1926	unknown	----	----	----	----	----	----
1927	1,100	41	30	----	----	----	----
1928	unknown	37	27	----	----	----	----
1929	unknown	57	49	----	----	----	----
1930	11,000	141	70	20,600	220	8,100	38
1931	unknown	418	415	23,000	266	12,500	183
1932	11,695	176	173	12,850	224	8,916	820
1933	30,000	231	----	10,000	152	6,085	34
	67,084	1,880	895	66,450	862	35,601	1,075

Secondly, large numbers of seedlings are raised from crosses that are designed to give information of use in making crosses or to furnish breeding stock for later use. When such seedlings are raised the number of selections from them is often relatively small.

In the third place, few of the selections made are finally introduced and the selections of the different years may, and to some extent do, represent different standards of judgment. Under the different weather conditions of different years in different parts of the country, the same standards cannot be used. Consequently far more seedlings that later prove inferior are saved in some years than in others. Thus under the weather conditions in North Carolina in 1932 nearly 10 per cent of the seedlings were saved while in 1930 and 1931 only about 1 per cent was saved.

Varieties Introduced

So far, seven varieties have been introduced, all from the earlier crosses. It is particularly interesting to note the relatively small number of seedlings in the lots from which they were selected.

Thus, five of the named varieties (Narcissa, Redheart, Dorsett, Bellmar, and Blakemore) came from 129 seedlings, and one other, the Fairfax from a small part of 383 seedlings that had become mixed and whose parentage was uncertain. No selections have yet been introduced from the large number of seedlings grown since 1925. These results show: (1) that the best selections so far introduced have come from very small numbers of seedlings and (2) that the great majority of the crosses have given no valuable seedlings. This is the more remarkable when we consider the commercial importance of the parents used in many of the crosses and the large number of seedlings ot some of the crosses that were given consideration.

The results of Klondike crosses may be taken as an example of the lack of outstanding seedlings from large numbers of crosses with the most important commercial shipping variety in the United States. In 1922 the first crosses with it fruited and some nine selections were made, none finally proving of value. In 1923 crosses were fruited as shown in Table V. Eighty-four selections from these crosses were saved but none has been found worth introducing.

In 1925 over 450 crosses with Klondike were fruited and three selections made from them, none of which has proved worth introducing. In recent years, 1930 to 1932, many thousands of additional crosses have been fruited at

TABLE V.—Results of Klondike crosses fruited in 1923.

Cross	Number of Seedlings
Dunlap × Klondike	560
Early Jersey × Klondike	24
Euresko × Klondike	200
Howard 25 × Klondike	300
Parsons × Klondike	42
Belt × Klondike	54
Burrill × Klondike	37

TABLE IV.—Parentage of the seven varieties introduced as a result of the breeding work of the U. S. Department of Agriculture, and the number of seedlings represented by each cross. (Note that Nos. 520 and 633 are selections from a single cross, as are also Nos. 655 and 659.)

Variety	U. S. D. A. No.	Cross	No. Seedlings
Southland	44	Ettersburg 80 × Howard 17	Probably not over 50
Narcissa	520	Royal Sovereign × Howard 17	31
Fairfax	613	Mixed seedlings	383 (a few of these came from the same cross from which Fairfax resulted)
Redheart	632	Portia × Euresko	51
Dorsett	633	Royal Sovereign × Howard 17	31
Bellmar	655	Missionary × Howard 17	47
Blakemore	659	Missionary × Howard 17	47

VARIETAL DIFFERENCES IN RESISTANCE

Figure 13

Great differences are noted in resistance to most of the pathogenic organisms and virus diseases to which the strawberry is subject. Above is shown the difference in reaction of two varieties to the "yellows" disease, a virus infection of great economic importance in certain strawberry growing regions of central California. On the left is shown a plant of the Marshall variety, which has quickly succumbed to the disease. On the right is a plant of the Bellmar variety which is relatively quite resistant to the "yellows." The Bellmar (U. S. D. A. 655) is one of the varieties which has been produced by the strawberry breeding discussed in this article.

the North Carolina and Maryland stations to explore thoroughly the possibility of utilizing the superior qualities of the Klondike in breeding. The more important of these crosses are listed in Table VI.

The number of selections in the different crosses with Klondike ranges from over 10 per cent in the cross of Bellmar × Klondike to less than half of one per cent for the 5,550 seedlings of the crosses between Klondike and Howard 17. The dominance of susceptibility to the "leaf-scorch disease" appears in most of the seedlings in a majority of the crosses. This, in addition to inheritance by its seedlings of

TABLE VI.—More important Klondike crosses of 1930 to 1932.

Cross	Number of Seedlings	Number of Selections
U.S.D.A. 652 × Klondike	4,100	37
Klondike × Howard 17	3,300	21
Howard 17 × Klondike	2,250	6
Klondike × Marshall	1,600	23
Blakemore × Klondike	600	25
Klondike × U.S.D.A. 778	300	26
Missionary × Klondike	250	3
Klondike × U.S.D.A. 817	250	3
Bellmar × Klondike	100	12
Klondike × U.S.D.A. 613	50	4
Totals	12,800	160

tender skin, sunken seeds, and often a peculiar flavor, has resulted in relatively few selections.

The Howard 17 (*Premier*) has proved to be just as fine as a parent as the Klondike has proved poor. Five and probably six of the seven new varieties already introduced have Howard 17 as one parent. The first selections made (in 1922) had 19 out of 100 with Howard 17 as one parent. Of all the selections still held at the United States Department of Agriculture station in Maryland, 340 or nearly 40 per cent have Howard 17 as one parent, while 373 are crosses, one parent of which was a selection coming from Howard 17 crosses. In addition, 147 selections are from crosses of Nos. 542 and 613 (both of unknown parentage but thought to be Royal Sovereign × Howard 17) with other varieties. Thirty-four of the selections are crosses of Howard Supreme (Howard 103 × Howard 17) with other varieties, while 53 are crosses of selections of which one parent resulted from Howard Supreme crosses.

Howard 17 is very resistant to leaf spot and leaf scorch under most conditions in northern states, and many of its seedlings are resistant also. It is productive, early, and the fruit is attractive. However, in crosses with very susceptible varieties the seedlings may not be resistant. For example, a cross of Howard 17 × Black Prince gave the following record:

Very susceptible to	Per cent
Leaf spot	53
Leaf scorch	11
Leaf spot and leaf scorch	7
Mildew	8
Mildew and leaf spot	5
Mildew and leaf scorch	7

Eight per cent were fairly resistant to all three of the diseases listed above.

In the southern part of the area where Howard 17 is grown, it is poorer in quality than farther north and its seedlings seem of poorer quality, also.

The New York Experiment Station (Geneva) has already published on the similar importance of Howard 17 in their breeding work.[4] It seems likely to be one of the outstanding varieties in the history of the strawberry in this country.

Summary of Principal Crosses and Selections

Because many of the crosses were represented by very small numbers of seedlings that actually fruited, only the crosses with the larger numbers of seedlings or which are of especial interest are listed in Table VII (page 458).

Besides the Royal Sovereign × Howard 17 cross and the Howard 17 crosses in general the outstanding crosses considered on the basis of relative number of selections are as given in Table VIII.

As indicated below, not all these crosses have come up to first expectations while many have not been tested sufficiently to indicate their real value. Most of this group, however, are crosses between varieties one of which has a tough skin and a solid flesh.

A few of the more important or interesting varieties used in breeding may be mentioned. U. S. D. A. 652 is a cross of Red Sugar × Howard 17 that is remarkable for resistance to leaf diseases, productiveness, and the beauty of its fruit. It is probably one of the most productive selections raised at the Maryland station but has the lowest dry weight and is one of the softest berries tested. It has proved of value

TABLE VIII.—Outstanding crosses in the strawberry breeding work to date.

Cross	Number of Selections	Approx. No. of Seedlings
Ettersburg 904 × Howard 17	28	300
Howard 17 × 632	24	100
Howard 25 × Klondike	38	300
Klondike × 778	52	600
Missionary × 613	109	900
Redheart (632) × Howard 17	41	300
Rockhill × Marshall	21	200
682 × 659	39	400
844 × 632	26	300
Howard 25 × Kalicene	10	31
Portia × Kalicene	15	76
842 × Kalicene	13	300
Kalicene × Howard 17		

TABLE VII.—List of the more important crosses, the approximate numbers of seedlings fruited (to nearest hundred), the number of selections and the year first fruited for 1923, 1925, 1930, 1931 and 1932; Maryland and North Carolina.

Cross-Variety or U.S.D.A. Number	Approx. No. of Seedlings	Number of Selections	Year Selected
Aroma × 542	200	3	1932
Bedarena × 520	200	0	1932
Bellmar × 542	600	4	1932
Bellmar × 613	100	19	1932
Bellmar × 659	200	3	1932
Bellmar × Klondike	100	12	1932
Blakemore × 542	1,300	75	1932
Blakemore × 613	400	38	1932
Blakemore × Deutsch Evern	200	1	1932
Blakemore × Ettersburg 121	500	7	1932
Blakemore × Howard 17	1,200	57	1932
Blakemore × Klondike	1,700	47	1931 & 1932
Blakemore × Marshall	400	2	1932
Blakemore × Royal Sovereign	100	5	1932
Chesapeake × 668	100	6	1932
Chesapeake × Aroma	100	17	1923
Chesapeake × Dunlap	100	15	1923
Cream × Parsons	200	0	1925
Delecto × Parsons	100	5	1925
Duluth × Belt	400	15	1923
Dunlap × 25	1,000	3	1930
Dunlap × Klondike	600	25	1923
Ettersburg 904 × Howard 17	300	28	1931
Ettersburg 80 × Klondike	100	1	1925
Euresko × Klondike	200	10	1923
Fragaria virginiana 27 × Rockhill	200	6	1925
Howard 17 × 542	1,200	18	1932
Howard 17 × 613	300	13	1931
Howard 17 × 632	100	24	1931
Howard 17 × 633	1,600	85	1931
Howard 17 × 624	1,000	25	1932
Howard 17 × 659	400	1	1931
Howard 17 × Klondike	2,200	6	1930 & 1931
Howard 17 × Marshall	400	3	1930
Howard 17 × *F. chiloensis*	500	4	1925
Howard 25 × Espoir	100	2	1925
Howard 25 × Ettersburg 80	100	9	1925
Howard 25 × Ettersburg 121	300	17	1925
Howard 25 × Hericart de Thury	100	3	1925
Howard 25 × Klondike	300	38	1925
Howard 25 × Kalicene	31	10	1925
Howard 25 × L. Gauthier	100	4	1925
Howard 25 × Royal Sovereign	200	9	1925
Klondike × 542	100	3	1932
Klondike × 613	50	4	1931
Klondike × 778	500	52	1931 & 1932
Klondike × 817	200	3	1931
Klondike × Howard 17	3,300	21	1930 & 1931
Klondike × Marshall	1,500	23	1931
Klondike × *F. chiloensis*	100	2	1925
Missionary × 542	1,400	83	1932
Missionary × 632	600	42	1932
Missionary × 613	900	109	1932
Missionary × 659	300	16	1932
Missionary × Deutsch Evern	200	0	1932
Missionary × Ettersburg 450	200	13	1932
Missionary × Howard 17	1,500	65	1931 & 1932
Missionary × Klondike	500	13	1931
Missionary × Marshall	400	6	1932
Portia × Ettersburg 121	200	1	1925
Portia × Ettersburg 450	100	4	1925
Portia × Kalicene	76	15	1925
Portia × Lnge	100	4	1925
Portia × Trebla	200	3	1925
Parsons × Ettersburg 121	100	0	1925
Parsons × Howard 17	200	1	1925
Redheart × Howard 17	300	41	1931
Rockhill × Azores var.	100	2	1929
Rockhill × Constante Fecunde	100	4	1925
Rockhill × Marshall	200	21	1929
F. chiloensis × 632	300	10	1930
U.S.D.A. 25 × 632	300	2	1930
U.S.D.A. 25 × Marshall	100	0	1930
U.S.D.A. 27 × Ettersburg 121	300	0	1932
U.S.D.A 542 × 659	200	3	1932
U.S.D.A. 631 × 25	200	1	1930
U.S.D.A. 652 × 542	700	28	1932
U.S.D.A. 652 × 613	1,500	59	1932 & 1931
U.S.D.A. 652 × 632	2,600	96	1932 & 1931
U.S.D.A. 652 × 659	1,500	12	1932 & 1931
U.S.D.A. 652 × 668	500	1	1932 & 1931
U.S.D.A. 652 × Ettersburg 450	400	10	1932 & 1931
U.S.D.A. 652 × Klondike	4,400	37+2	1932 & 1931
U.S.D.A. 652 × Missionary	500	0	1931
U.S.D.A. 682 × 659	400	39	1932
U.S.D.A. 694 × 542	600	0	1932
U.S.D.A. 694 ×659	200	2	1932
U.S.D.A. 694 × 632	500	2	1932
U.S.D.A. 778 × 613	600	22	1930 & 1931
U.S.D.A. 778 × 659	600	6	1931
U.S.D.A. 822 × 668	300	1	1932
U.S.D.A. 822 × Ettersburg 450	200	0	1932
U.S.D.A. 842 × Kalicene	300	13	1930
U.S.D.A. 844 × 632	300	26	1930 & 1931
U.S.D.A. 874 × 542	100	3	1932
U.S.D.A. 874 × 659	200	2	1932

in breeding for disease resistance but its seedlings usually produce soft fruit.

Fragaria virginiana 27 is a selection of the wild strawberry of Eastern North America, found by D. N. Shoemaker at Highland, North Carolina. It has been useful in breeding for productiveness, with high branching fruit clusters, but the berries of the selections have been soft. Ettersburg 450 is itself an almost ideal berry in size, shape, appearance, flavor, firmness, and health of plant but it is decidedly unproductive. Its seedlings have also been rather shy bearers.

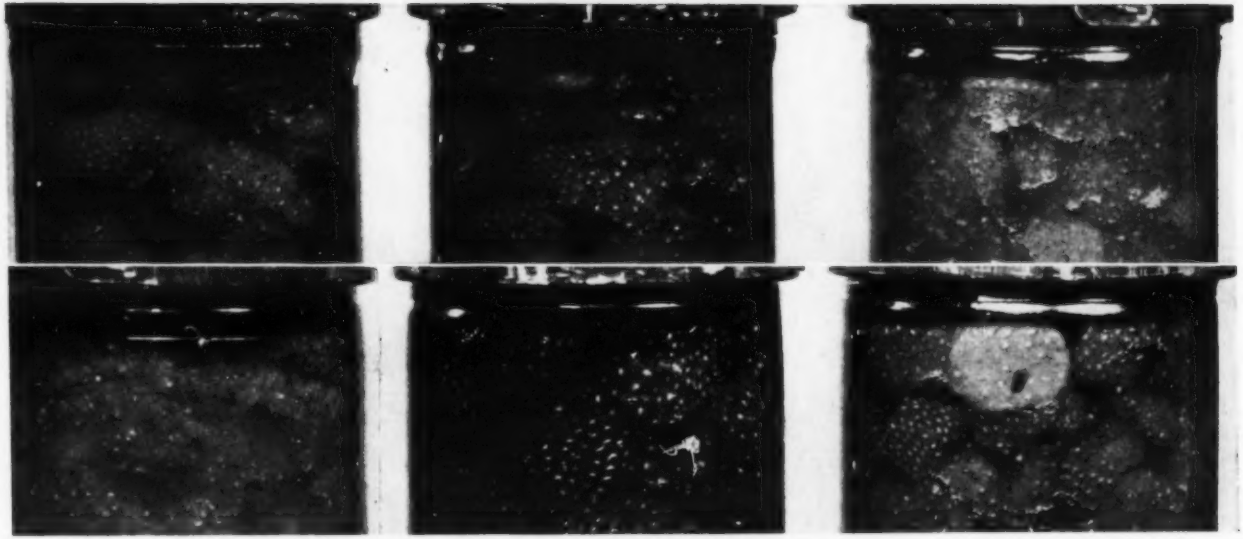
Royal Sovereign, though it has given good results in breeding, has itself died out from leaf diseases. Ettersburg 904 has been useful in breeding firm, late varieties of high dessert quality, but its fruits are small. Fairfax and Redheart are firm and larger than Ettersburg 904 but too dark. Many seedlings of these two varieties are of excellent dessert quality, those having Fairfax as one parent being mild and free from leaf spot, and those having Redheart as one parent being more acid but subject to leaf scorch and leaf spot. Kalicene has a solid flesh but a tender skin on a small berry. Seedlings from it have very fine quality, and some are firm. Most of them have a tender skin and are small in size. Southland has a solid flesh, high dessert quality, uniform shape, attractive appearance, and foliage remarkably resistant to leaf diseases, but the skin is tender. It has been found very useful for breeding for southern regions. U. S. D. A. 542, which is of unknown parentage, but may be a sister to Narcissa, has exceptionally firm-fleshed, tough-skinned fruit that does not rot readily and has been repeatedly selected as the handsomest and one of the best in quality. Unfortunately it is not very productive and is very subject to leaf diseases. Its seedlings inherit unusual susceptibility to leaf diseases and often a tough skin.

In 1928 the small fruit work of the Oregon Agricultural Experiment Station was reorganized to include cooperative work with the U. S. Department of Agriculture. The first strawberry crosses to fruit in Oregon resulting from this cooperative work were some 20,000 seedlings in 1930. From these 148 selections of variety crosses and 72 selections of crosses of varieties and species for later breeding were obtained. In 1931 some 23,000 seedlings were fruited and 266 selections were made. In 1932 from some 10,800 seedlings 224 selections were made. A summary of the principal crosses at the Oregon Station with the number of selections from each is given in Table IX.

It will be noted that the parentage of the seedlings in Oregon is quite different from that of the Maryland and of the North Carolina seedlings. The selections in Oregon have been made quite largely with a few specific objects in mind. A large number was selected for further testing and some showing desirable characters, but not themselves up to standard, were kept as parents of later crosses. Thus the selections,

TABLE IX.—List of more important crosses in Oregon with the approximate number of seedlings fruited and the number of selections for 1930-1932.

Crosses	Number seedlings	Number selections
Blakemore × Marshall	1,211	35
Blakemore × Ettersburg 121	820	5
Clark × Narcissa	480	28
Corvallis × Ettersburg 121	341	2
Ettersburg 121 × O.S.C. 2	1,484	5
Ettersburg 121 × O.S.C. 33	1,338	0
Ettersburg 121 × O.S.C. 39	1,696	32
Ettersburg 121 × O.S.C. 60	541	1
Ettersburg 121 × Magoon	1,925	1
Ettersburg 121 × Marshall	1,467	10
Ettersburg 121 × Narcissa	532	8
Gold Dollar × Marshall	591	10
Gold Dollar × Narcissa	373	13
Gold Dollar × O.S.C. 60	542	18
Marshall × Ettersburg 121	840	18
Marshall × O.S.C. 7	460	3
Marshall × O.S.C. 10	566	4
Marshall × O.S.C. 57	550	7
Marshall × O.S.C. 60	349	11
Marshall × Clark	415	2
Marshall × Narcissa	987	22
Marshall × Redheart	798	24
Narcissa × Marshall	663	12
Narcissa × O.S.C. 57	592	6
Redheart × Ettersburg 121	512	9



VARIATION IN SUITABILITY FOR PRESERVING

Figure 14

The upper row shows the reaction of three selections in which the fruit is to be used for topping for ice cream. The variety in the jar at the right is distinctly less desirable than the other two. Below are shown preserved samples of three selections tested for use in making preserves. Some of these lose their color on heating (sample at right); others mash badly (lower left); and some remain too dark (lower center). The selection at the upper left is the best adapted for preserving. If selections are satisfactory in these preserving tests and also in field performance they are subjected to further extensive tests before being introduced as named varieties. Only a small fraction of one per cent of the original selections succeeds in passing these tests.

crosses of *Fragaria chiloensis* and *F. cunefolia* with cultivated varieties are being studied for later use in breeding, especially to obtain hybrid vigor, resistance to rhizoctonia root rot and to drought, and for their habit of winter growth, and winter flower bud development. Since both species are, chiefly at least, black seeded and are not attractive when canned, preserved or frozen, the parents being used to cross with the F_1 are mostly yellow seeded.

The crosses in Oregon have included (1) crosses of varieties now raised in the Northwest, (2) crosses of varieties in the Northwest with eastern and European varieties (3) crosses with selections of species. Not only have varieties in the Northwest been crossed but selections of the F_1 have been backcrossed with their parents, and sister plants have been crossed. Such line breeding has been found to reduce the vigor of the seedlings very markedly. Except as it may be found desirable to breed toward pure lines of definite type and for an understanding of the genetic constitution of varieties the method has been of no economic value as yet. More promising results have been obtained in crosses between varieties adapted to the Northwest and with eastern varieties, and with selections from the Maryland station. As a measure of the relative vigor of inbred and outbred seedlings the average weight of four to ten mother and runner plants in November was calculated as in Table X.

A study of the usefulness of some varieties and of the effect of one variety on another may be made as in Table XI. Each variety is listed as a female and male parent.

It is apparent that certain crosses gave poor results with some parents and good results with others. Thus Clark × Marshall and Clark × some other varieties gave no selections while Clark × Narcissa gave 5.83 per cent selections. That some varieties might prove better as pollen parents than as seed parents (or the converse) is hardly borne out by the figures though some varieties seemed slightly better as one or the other parent. Considering all crosses, Marshall was a poor pollen parent in nine cases and in thirteen cases a poor seed parent; it was a good and in some cases excellent pollen parent in six instances and in five instances gave the same results when used as a seed parent.

When two selections (cross 2) having one parent the same were crossed, the resulting seedlings were more vigorous than when one of the selected

TABLE X.—Comparison of crossing closely related varieties, back-crossing and out-crossing in green weight of plants with runners attached.

Cross	Parentage	Av. Weight of Plants	% of Largest, No. 4
1	Ettersburg 121 × O.S.C. 7 (Ettersburg 121 × Wilson) (F_1 × one parent	358	74
2	O.S.C. 14 (E. 121 × Marshall) × O.S.C. 7 (E. 121 × Wilson) (F_1 × F_1 where one parent is the same)	426	88
3	Redheart × O.S.C. 7 (F_1 × unrelated)	441	91
4	Ettersburg 121 × *F. cuneifolia* (F_1 × unrelated species)	486	100

TABLE XI.—Comparison of value of some varieties of strawberries in crossing when used as male (at top) and as female (vertical at left) parents (evaluated in per cent of seedlings selected).

	Ettersburg 121	O. S. C. 7	Clark	Marshall	Narcissa	Redheart
Ettersburg 121	—	.59	1.81	.85	1.50	2.34
O.S.C. 7	.49	—	—	.64	1.01	—
Clark	—	2.07	—	—	5.83	—
Marshall	1.51	.88	.48	—	2.68	2.88
Narcissa	1.97	—	—	1.81	—	—
Redheart	1.99	1.69	—	2.05	—	—

varieties was back-crossed with one parent (cross 1), but not so vigorous as when crossed with an unrelated variety (cross 3) or with an unrelated species (cross 4).

In general Marshall has proved to be an excellent parent and may be used to add quality, aroma, size, and possibly to increase the sugar content. Narcissa has also proved to be an excellent parent especially to give uniform shape and size, exceptional beauty and quality, and possibly preserving quality. Redheart has proved to be a fine parent to add firmness and canning quality. U. S. D. A. 682 has given seedlings of very fine preserving color. Magoon and Gold Dollar have not proved to be satisfactory. Ettersburg 121 has proved desirable only in breeding for canning varieties.

Summary

Reviewing the work to date, as a result of the breeding work from 1920 to 1925, seven varieties have been introduced, one (Southland) as a home garden variety for the South, a second (Redheart) as a canning variety for the Pacific Northwest, and five as general market varieties. Four of these seven, Southland, Dorsett, Fairfax, and Narcissa, were selected as better dessert varieties than were raised in the regions to which they were adapted. These varieties represent attempts to solve the problems in mind at the beginning of the work. A large part of the selections of more recent years and now under test represent other objectives. In general, these are to obtain varieties adapted to the requirements of different regions of the country, varieties resistant to various pests, varieties with a bright, light color like that of the Blakemore which does not darken after picking, and varieties with as firm fruit as that of the Fairfax.

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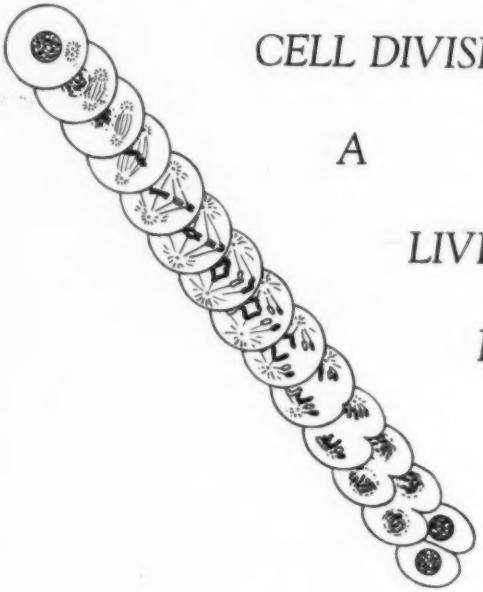

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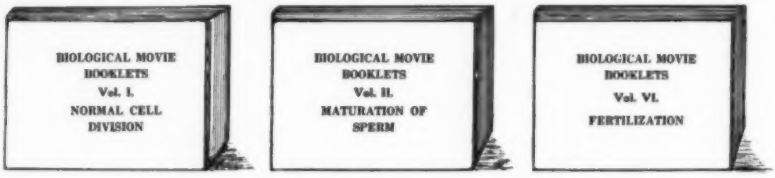

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